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# CHANGES IN WINTER WHOOPING CRANE TERRITORIES AND RANGE 1950-2006

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***Abstract:*** The whooping crane (*Grus americana*) winters on the Texas coast primarily in salt marsh habitat. The location of adult whooping crane winter territories during 9 winters between 1950 and 2006 was derived from aerial census data digitized onto infrared photos using GIS software. Range expansion, including changes in distribution and size of winter territories, was analyzed over a 57-year period as flock size increased by 765%. Crane pairs have opted to establish territories in or close to the traditional winter area rather than moving long distances along the coast. This distribution seems based on the preference of the male crane to establish a territory as close as possible to its parents. Colonizing occurred to the nearby areas of Matagorda Island in 1958, San Jose Island in 1969, Lamar Peninsula in 1971, and Welder Flats in 1973. Minimum territory sizes were calculated to be 101 ha for Aransas National Wildlife Refuge and West St. Charles Bay, 139 ha for Welder Flats, 204 ha for Matagorda Island and Welder Flats, and 304 ha for San Jose Island. Salt marsh habitat was measured to determine if enough winter area is present to reach recovery targets and to predict expected use patterns for the near future. Based on an average winter territory size of 172 ha, the current winter range and contiguous areas can support up to 576 whooping cranes. Additional salt marsh habitat was measured in a 111-km radius from Aransas National Wildlife Refuge. If suitable, this non-contiguous area could support an additional 580 whooping cranes to reach a total flock size of 1,156. However, with the Texas coast undergoing rapid development and sea level rise, there is insufficient protected habitat for whooping cranes to reach recovery targets.

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**Key words:** development, *Grus americana*, territories, whooping crane, winter range.

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The only naturally occurring flock of whooping cranes (*Grus americana*) winters on the central Texas coast between Port Aransas and Port O'Connor, Texas, at Aransas National Wildlife Refuge (NWR) and vicinity. The year of the endangered whooping crane is divided between the United States (October-April) and Canada (April-October). While in Canada, the birds nest and raise their young in Wood Buffalo National Park and vicinity on the Alberta/Northwest Territories border.

Starting in the 1950s, the Aransas NWR conducted periodic aerial census flights over the coastal marshes during the period when cranes were present. In many winters, flights were conducted on a weekly basis. Crane locations were plotted on maps or more recently on aerial photos. Surveys documented annual flock size, productivity, winter range, habitat use, and mortality.

This study analyses the changes in distribution and size of winter territories over a 57-year period, and updates the analysis done by Stehn and Johnson (1987). It predicts expected patterns of use for the near future and measures habitat currently available in the winter area to determine if enough habitat is present to reach recovery targets.

## STUDY AREA

The whooping crane winters in coastal salt marsh habitat in the San Antonio-Guadalupe and Mission-Aransas River estuaries. Salt marsh is present on western portions of the barrier islands of San Jose and Matagorda and on the edges of the mainland at Aransas NWR, Lamar Peninsula, and Welder Flats (Fig. 1). Aransas NWR and Welder Flats are situated across San Antonio Bay approximately 7 and 9 km, respectively, west of the crane range on the barrier islands. The Lamar Peninsula is located 1.4 km across St. Charles Bay west of Aransas NWR. The Tatton Unit of the Aransas NWR is located on the west side of St. Charles Bay immediately north of the Lamar Peninsula. “West St. Charles” refers to salt marsh areas on the Lamar Peninsula and/or Tatton Unit. In this paper, “Aransas” refers to the entire wintering area. “Aransas NWR” refers only to the portion of the refuge located on Blackjack Peninsula between San Antonio Bay and St. Charles Bay.

## METHODS

From observations made on periodic census flights of exclusive use of an area by an adult crane pair or family

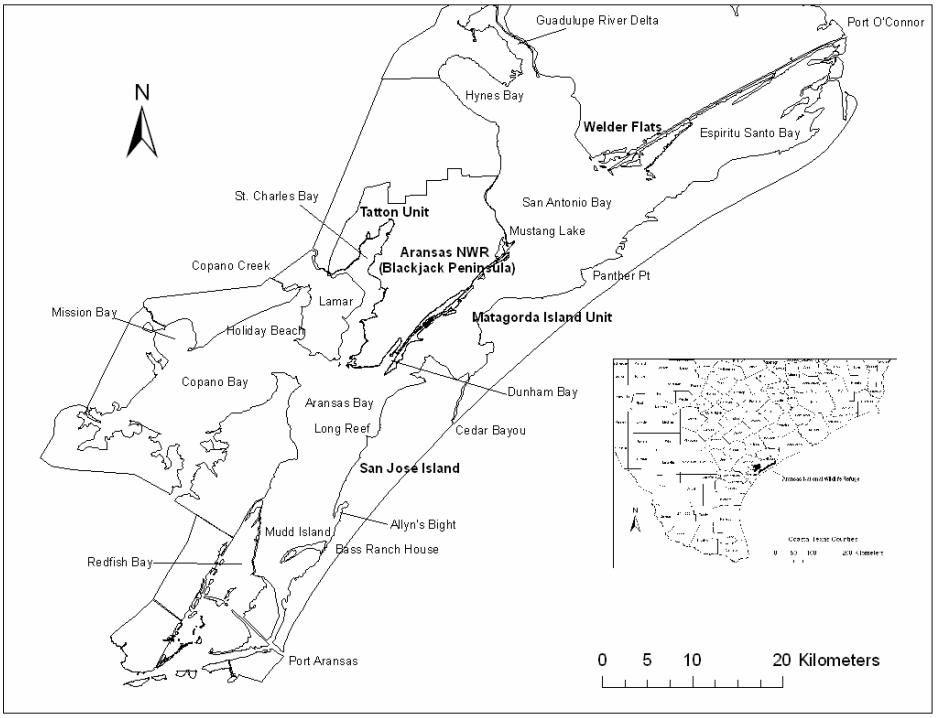


**Figure 1. Whooping crane winter area at Aransas.**

group, whooping crane territories were delineated following the methodology of Stehn and Johnson (1987). Locations of a pair were excluded when in a neighbor's territory or in upland areas. Occasional pairs that roamed extensively and did not defend a territory were excluded from the data analysis. Territory locations for the winters of 1950, 1961, 1971, and 1979 were taken from Stehn and Johnson (1987). Data were taken directly from census flight maps for the winters of 1985, 1990, 1995, 2001, and 2006. Winter was defined as the period from October to April. Territory maps were digitized onto color infrared aerial imagery and measured using ArcGIS 9.2 software (ESRI, Redlands, CA).

Adult pairs typically returned annually to the same territories based on information from banded birds (Stehn and Johnson 1987). Because of small sample size, areas were added where a territorial pair had been observed in previous years. For consistency, areas of upland habitat and bay water too deep for cranes to use were excluded from delineated territories. In some cases, this redefinition created territory size smaller from those presented by Stehn and Johnson (1987) but was a better indicator of the area of salt marsh actually used. "Colonization" was defined as the establishment of a territory in a non-contiguous part of the winter area where no other territories were present.

We estimated future crane densities using only data from territorial pairs with adjacent territorial pairs when calculating average territory size. Larger crane territories at the ends of the crane range were excluded. Territories on Aransas NWR and West St. Charles were combined due to their similar values and small sample size on West St. Charles. Average minimum territory sizes for each part of the crane range were taken to be the lowest value measured between 1950 and 2006, and for the entire range the lowest value between 1985 and 2006.

## RESULTS

### Number and Location of Territories

Records from the late 1800s and early 1900s placed whooping cranes in salt marshes at Aransas on the mainland and barrier islands (Allen 1952). When Aransas NWR was established on the Blackjack Peninsula (Fig. 1) in 1937, a flock of 18 birds wintered on the refuge. A few of these whooping cranes were occasionally seen on San Jose and Matagorda Islands and Welder Flats (Stevenson and Griffith 1946).

When census flights began in 1950, all delineated

**Table 1. Number of whooping crane territories in different parts of the winter range at Aransas.**

| | 1950 | 1961 | 1971 | 1979 | 1985 | 1990 | 1995 | 2000 | 2006 | 2007[a] |
|---|---|---|---|---|---|---|---|---|---|---|
| Aransas NWR | 7 | 8 | 11 | 10 | 15 | 18 | 17 | 19 | 20 | 20 |
| W. St Charles | 0 | 0 | 1 | 1 | 1 | 1 | 4 | 2 | 2 | 3 |
| San Jose | 0 | 0 | 1 | 2 | 4 | 5 | 8 | 11 | 16 | 16 |
| Matagorda | 0 | 1 | 4 | 3 | 6 | 9 | 16 | 17 | 22 | 25 |
| Welder | 0 | 0 | 0 | 2 | 2 | 4 | 4 | 8 | 6 | 8 |
| Totals | 7 | 9 | 17 | 18 | 28 | 37 | 49 | 57 | 66 | 72 |

[a] T. Stehn, unpublished data.

territories ($n$ = 7) were located on Aransas NWR (Stehn and Johnson 1987) (Table 1). Six of these territories were spread along the eastern edge of the refuge between Mustang Lake and Dunham Bay (Fig. 2). One territory was located on St. Charles Bay on the west side of the refuge at Egg Point. The number of territories at Aransas NWR increased progressively to 18 in 1990, but then increased to 20 in 2006. With much of the contiguous refuge habitat occupied, the rate of establishment of additional territories on the refuge slowed as had been predicted by Stehn and Johnson (1987). Instead, new crane pairs colonized into nearby non-contiguous areas.

All colonization occurred into suitable habitat close to the occupied range. Territories in non-contiguous areas were first established on Matagorda Island in 1958, San Jose Island in 1969, Lamar in 1971, and Welder Flats in 1973 and have remained occupied to the present time. The first territories in those areas were located across open bays 6.7, 1.4, 6.3, and 13.2 km, respectively, to the closest portions of those areas to Aransas NWR. Dispersal followed an orderly progression outwards from the core area.

Colonizing new areas generally does not occur unless available habitat in an occupied area is becoming limited

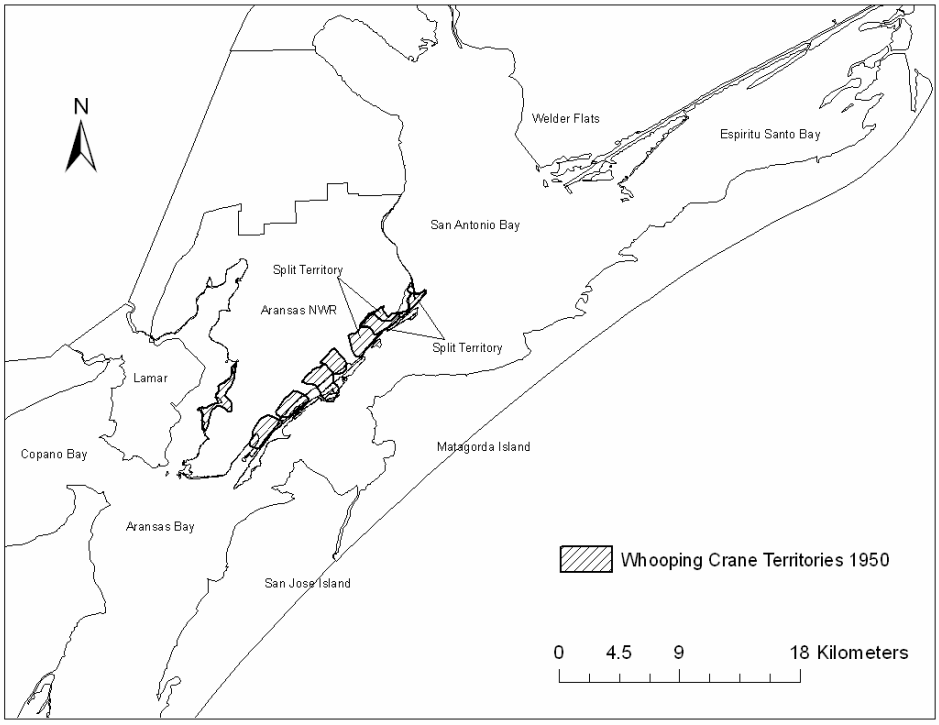


**Figure 2. Whooping crane territories at Aransas in 1950.**

**Table 2. Southwest to northeast maximum distance (km) of whooping crane territories in different parts of the winter range.**

| | 1950 | 1961 | 1971 | 1979 | 1985 | 1990 | 1995 | 2000 | 2006 | Length of occupied range in 2007[a] (km) | Length of available habitat[b] (km) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Aransas NWR | 17.5 | 18.4 | 21.9 | 22.2 | 23.1 | 22.6 | 22.4 | 23.1 | 21.2 | 22.9 | 23.1 |
| San Jose | 4.7 | 4.7 | 12.4 | 12.4 | 12.4 | 12.4 | 19.4 | 22.6 | 19.8 | 24.8 | 36.7 |
| Matagorda | 3.0 | 18.1 | 13.2 | 19.8 | 26.1 | 26.1 | 30.6 | 28.1 | 32.1 | 43.1 | 55.7 |
| Welder | | | | 3.9 | 9.4 | 10.8 | 11.4 | 21.9 | 21.4 | 23.2 | 26.4 |

[a] Occupied range includes territories plus areas where subadult crane use occurs.
[b] Available habitat includes occupied range plus contiguous unoccupied salt marsh

with little unoccupied contiguous habitat present. The percent of occupied habitat at Aransas NWR when colonization to other areas occurred as reflected by the ratio of linear distance of occupied marsh to total marsh available was 79.7% in 1961 and 94.8% in 1971 (Table 2).

The total number of territories for the 9 winters analyzed increased steadily from 7 to 66 between 1950 and 2006. The flock grew 765% from 31 to 237 birds during this same time period (Table 3). As the number of territories in all parts of the wintering area has grown, increasingly more territories became established in areas other than Aransas NWR. In 1958, census flights found consistent use of Matagorda Island with at least 1 territory present (Aransas NWR files, unpublished data), the first territory to be documented off Aransas NWR. Territories on Matagorda have continued to increase from 4 in 1971 to 25 territories in 2007 (Figs. 3-10).

In 1969, with 58 birds in the flock, 1 family group spent time on San Jose Island, the first territory noted on that part of the winter range (Aransas NWR files, unpublished data). A second territory was established on San Jose in 1979. Territory numbers on San Jose continued to climb from 4 to 16 between 1985 and 2007. Territories at Welder Flats have increased from 1 in 1973 to 8 in 2007. The first territory on Lamar Peninsula was established in 1971. Territories on the west side of St. Charles Bay peaked at 4 in 1995, with 2 territories on Lamar and 2 territories on the Tatton Unit. Currently, there are no territories present on the Tatton Unit. Furthermore, the number of territories on West St. Charles declined to 2 in 2000, the only area where territories are not currently at peak numbers based on territories delineated during 2007. A third territory, however, was established on Lamar in 2007.

The percentage of whooping crane territories on Aransas NWR has decreased from 100% in 1950 to 27.8% in 2007 (Table 4). The percentage of territories on all other areas increased, beginning in 1961. In 2007, Matagorda Island held the most whooping crane territories (34.7%). San Jose (36.9%) and Matagorda (32.7%) Islands had the

**Table 3. Number and total size of whooping crane territories at Aransas, 1950 to 2006.**

| Winter | Flock size | Total no. territories | Total territory size (ha) | Average territory size (ha) | Hectares per adult bird |
|---|---|---|---|---|---|
| 1950 | 31 | 7 | 2,199 | 314 | 157 |
| 1961 | 36 | 9 | 1,901 | 211 | 106 |
| 1971 | 59 | 17 | 4,904 | 288 | 144 |
| 1979 | 76 | 18 | 3,973 | 221 | 110 |
| 1985 | 84 | 28 | 8,121 | 290 | 138 |
| 1990 | 146 | 37[a] | 8,427 | 228 | 114 |
| 1995 | 158 | 49[b] | 14,017 | 286 | 143 |
| 2000 | 180 | 57[b] | 11,145 | 196 | 98 |
| 2006 | 237 | 66[b] | 13,889 | 210 | 105 |

[a] Six adult pairs were excluded due to extensive roaming, no defined territory, or loss of a mate during winter.
[b] One additional family group was present but did not have a defended area.

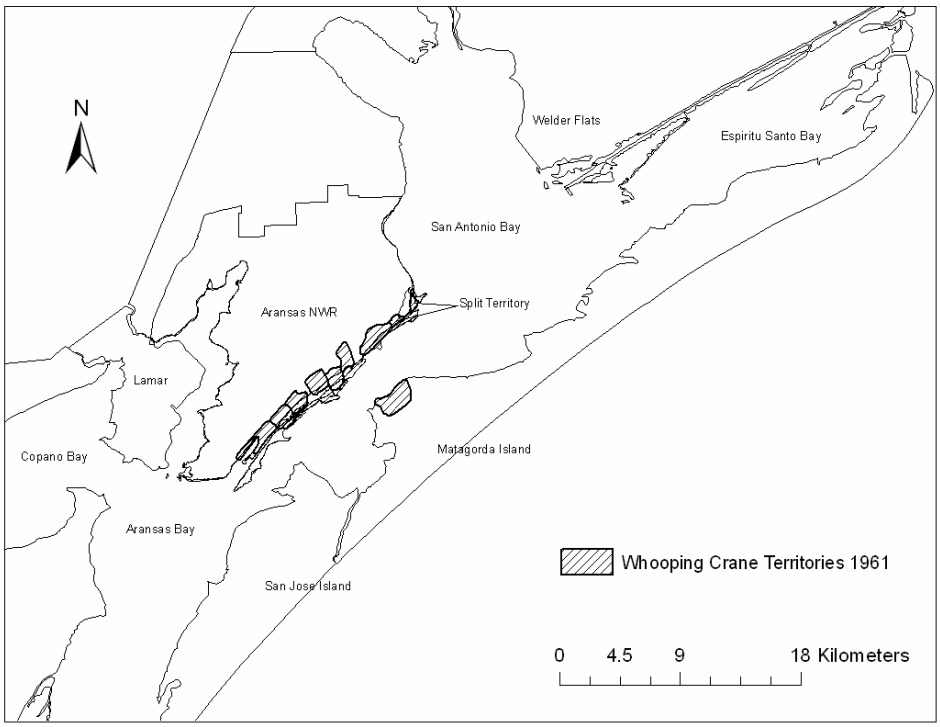


**Figure 3. Whooping crane territories at Aransas in 1961.**

**Table 4. Percentage of whooping crane territories in different parts of the winter range at Aransas and total range in hectares and percent in 2007.**

| | 1950 | 1961 | 1971 | 1979 | 1985 | 1990 | 1995 | 2000 | 2006 | 2007 | Species range[a] in 2007 (ha) | Species range[a] in 2007 (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Aransas NWR | 100 | 88.8 | 64.7 | 55.6 | 53.6 | 48.6 | 34.7 | 33.3 | 30.3 | 27.8 | 2,622 | 11.3 |
| W. St Charles | 0 | 0 | 5.9 | 5.5 | 3.6 | 2.7 | 8.2 | 3.5 | 3.0 | 4.2 | 399 | 1.7 |
| San Jose | 0 | 0 | 5.9 | 11.1 | 14.3 | 13.5 | 16.3 | 19.3 | 24.2 | 22.2 | 8,576 | 36.9 |
| Matagorda | 0 | 11.2 | 23.5 | 16.7 | 21.4 | 24.3 | 32.6 | 29.8 | 33.3 | 34.7 | 7,599 | 32.7 |
| Welder | 0 | 0 | 0 | 11.1 | 7.1 | 10.8 | 8.2 | 14.0 | 9.1 | 11.1 | 4,044 | 17.4 |
| | | | | | | | | | | | Total 23,240 | 100.0 |

[a] Species range includes territories, as well as areas used by subadults outside of territories.

highest percentages of occupied range.

The southwest to northeast linear distance between ends of the crane range in different parts of the wintering area increased over the years as new territories were established. From 1950 to 2006, the linear distance of the crane territories on Aransas NWR increased from 17.5 km to only 21.2 km while the number of territories increased from 7 to 20. Linear expansion was more dramatic on San Jose Island (4.7 to 19.8 km), Matagorda Island (3.0 to 32.1 km), and Welder Flats (3.9 to 21.4 km).

## Size of Territories

Between 1950 and 2006, the total area of territories increased from 2,199 ha to 13,889 ha (+632%), but did not rise steadily. Hectares occupied per adult bird varied between 98 and 157 (Table 3).

As the number of territories increased, the average winter territory size decreased from 314 ha in 1950 to 210

**Table 5. Average territory size (ha) in different parts of the whooping crane winter range, 1950-2006.**

| | 1950 | 1961 | 1971 | 1979 | 1985 | 1990 | 1995 | 2000 | 2006 |
|---|---|---|---|---|---|---|---|---|---|
| All areas | 314 | 211 | 289 | 221 | 290 | 216 | 279 | 195 | 210 |
| Aransas NWR | 314 | 190 | 155 | 156 | 179 | 108 | 145 | 101 | 109 |
| W. St Charles | | | 389 | 130 | 382 | 158 | 312 | 125 | 110 |
| San Jose | | 381 | 955 | 436 | 580 | 493 | 436 | 350 | 338 |
| Matagorda | | | 465 | 281 | 367 | 270 | 324 | 207 | 211 |
| Welder Flats | | | | 284 | 264 | 306 | 409 | 200 | 239 |

ha in 2006 (Table 5, Fig. 11). Excluding the "end" territories, the average size of all territories in 2006 (196 ha) was similar to the average territory size of 182 ha in 1961 (Table 6). At Aransas NWR, territories decreased from an average of 313 ha in 1950 to 108 ha in both 1990 and 2006. When the population was small and available habitat was abundant, adult pairs roamed over larger areas and defended larger territories. As crane numbers increased, more territories were established close to existing territories and crane movements were restricted by neighboring pairs defending their own territories.

Crane territories at the ends of the different areas of the crane range were usually larger next to unoccupied habitat, with no neighboring pairs on 1 side to restrict movements (Stehn and Johnson 1987). The average size of territories excluding end territories was 20.6% smaller than the average size of all territories (T. Stehn, unpublished data). This was calculated by averaging the 9 winters in the data set. Differences ranged between 0.3% less in 1950 and 61.4% less in 1971.

Territory size varied considerably over time in different parts of the crane winter range. For all years analyzed, the difference between the largest and smallest territories was considerable (Table 7). In

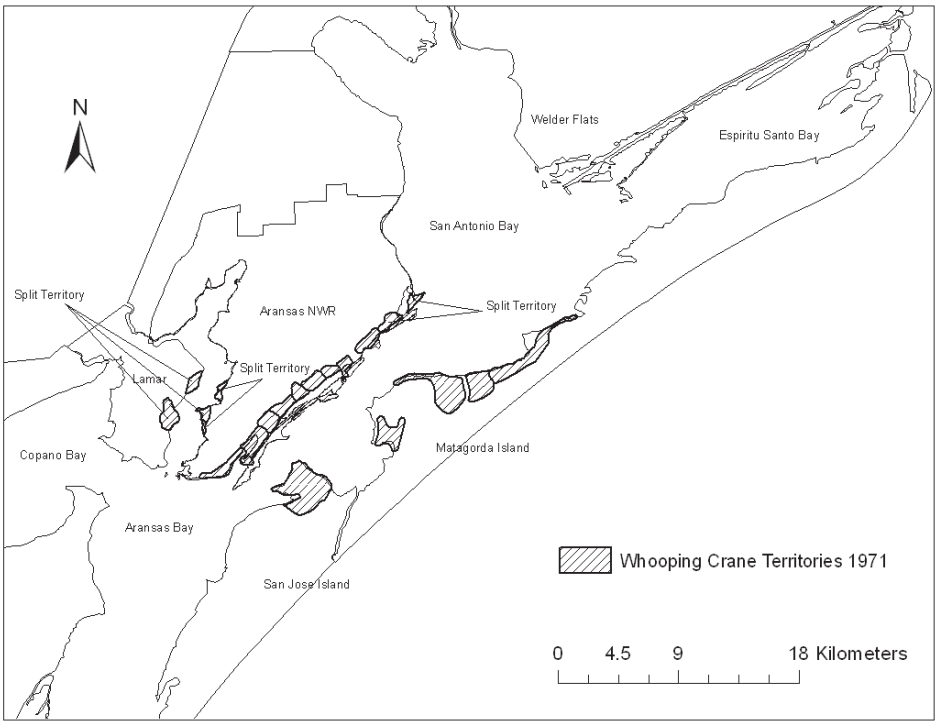


**Figure 4. Whooping crane territories at Aransas in 1971.**

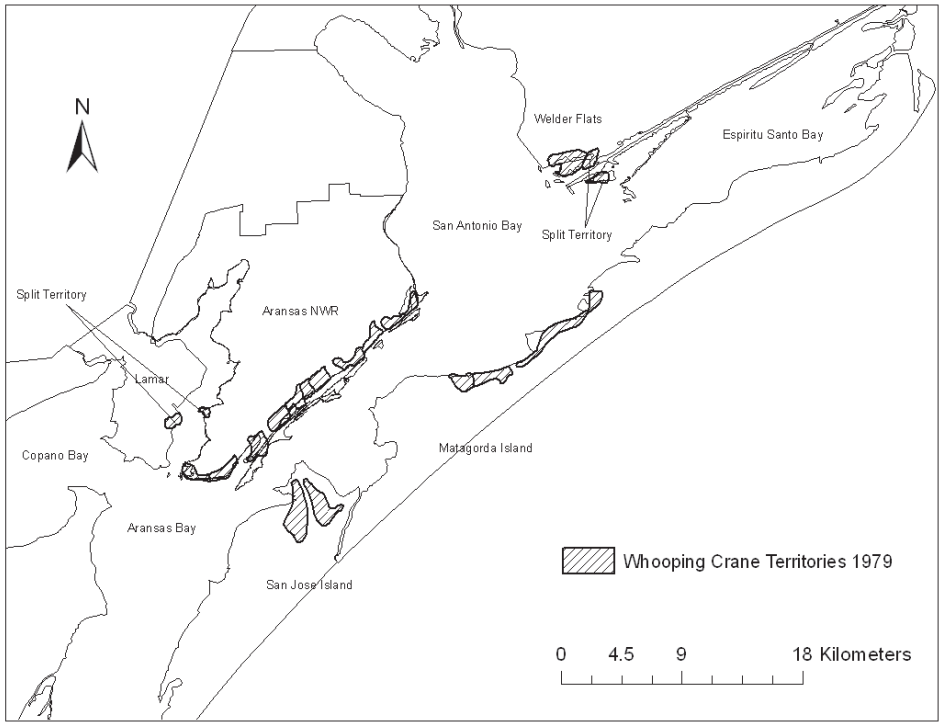


**Figure 5. Whooping crane territories at Aransas in 1979.**

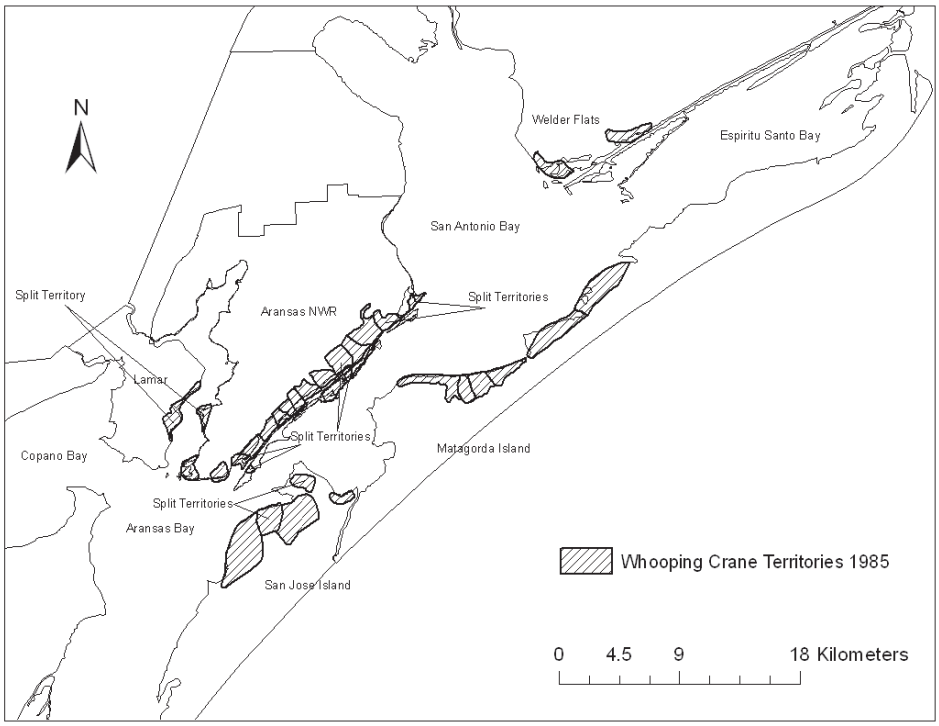


**Figure 6. Whooping crane territories at Aransas in 1985.**

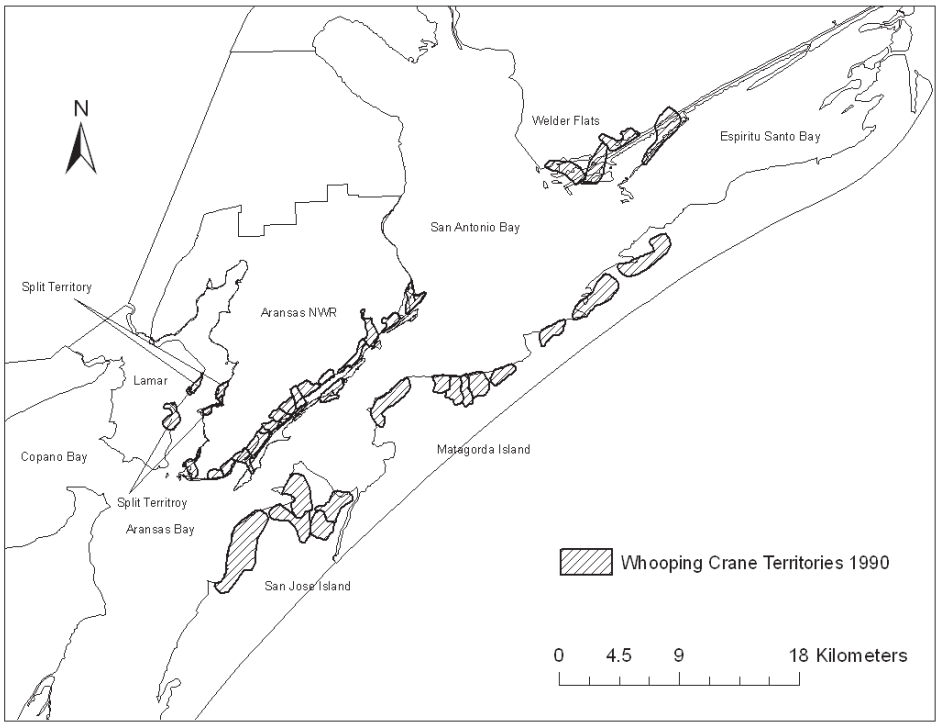


**Figure 7. Whooping crane territories at Aransas in 1990.**

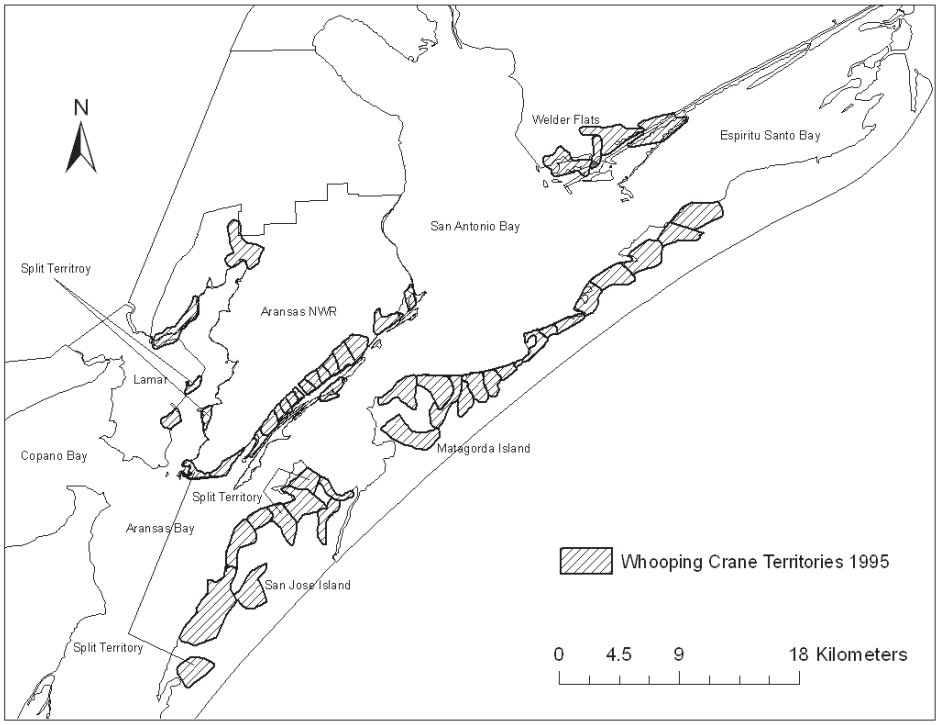


**Figure 8. Whooping crane territories at Aransas in 1995.**

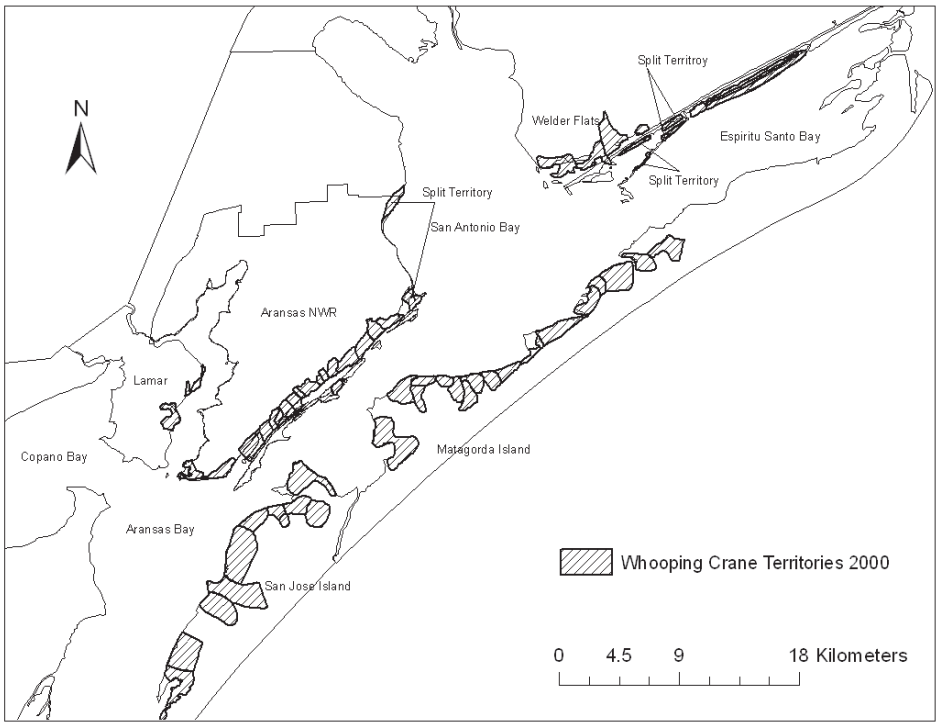


**Figure 9. Whooping crane territories at Aransas in 2000.**

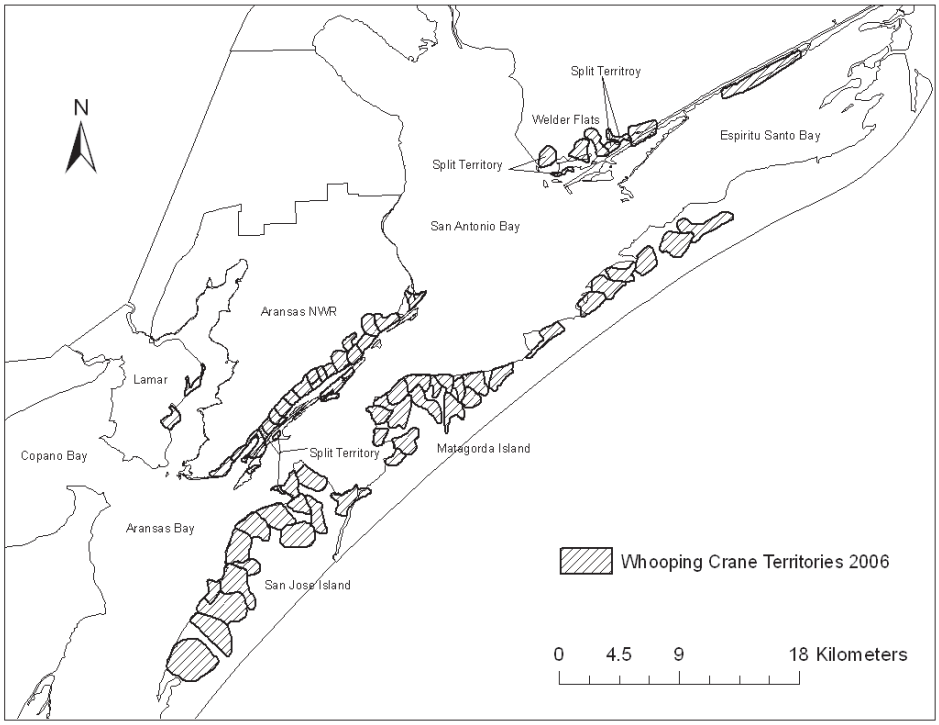


**Figure 10. Whooping crane territories at Aransas in 2006.**

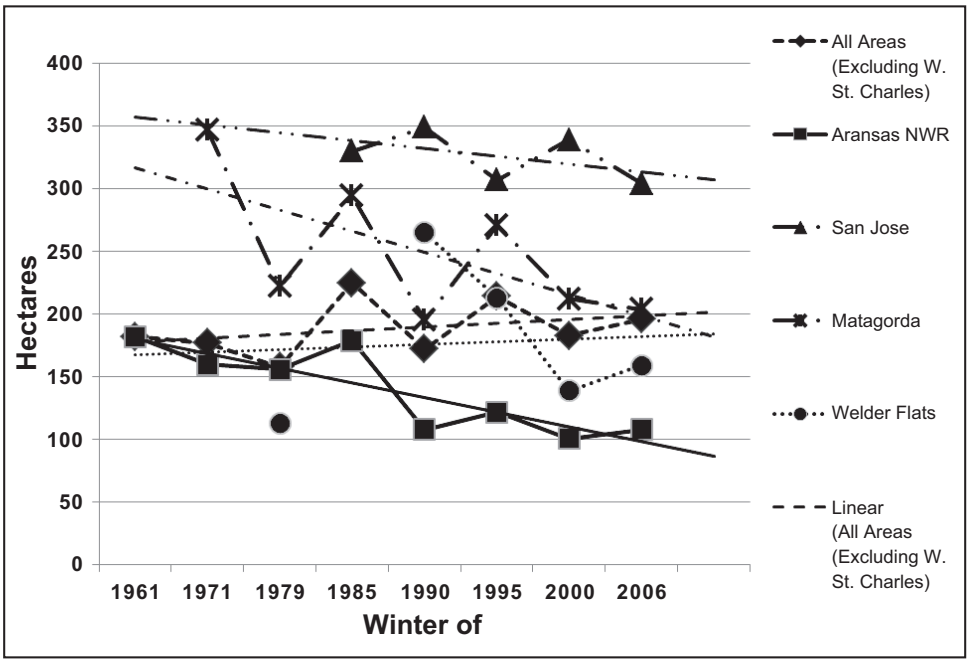


**Figure 11. Size of whooping crane territories, excluding end territories, in the different wintering areas at Aransas, 1961-2006.**

**Table 6. Average territory size (ha) excluding territories on the ends in the different parts of the whooping crane winter range from 1950 to 2006.**

| | 1950 | 1961 | 1971 | 1979 | 1985 | 1990 | 1995 | 2000 | 2006 |
|---|---|---|---|---|---|---|---|---|---|
| All areas[a] | 313 | 182 | 177 | 158[b] | 236 | 172 | 214 | 183 | 196 |
| Aransas NWR | 313 | 182 | 160 | 156 | 179 | 108 | 122 | 101 | 108 |
| W. St Charles | | | | | | | | 125 | 110 |
| San Jose | | | 347 | 222 | 439 | 349 | 307 | 339 | 304 |
| Matagorda | | | | 113[c] | 294 | 221 | 271 | 212 | 204 |
| Welder Flats | | | | | | 265 | 213 | 139 | 159 |

[a] Excludes West St. Charles Bay from analysis.

[b] Data excluded in estimating minimum territory size since 10 of the 12 territories were on Aransas NWR where territories are smaller than in all other parts of the crane range.

[c] Data excluded from analysis since only 1 territory..

**Table 7. Largest and smallest territory sizes (ha) and location at Aransas for 9 winters analyzed between 1950 and 2006.**

| Winter | Largest territory (ha) | | Smallest territory (ha) | |
|---|---|---|---|---|
| 1950 | Aransas NWR | 382 | Aransas NWR | 221 |
| 1961 | Matagorda Island | 381 | Aransas NWR | 106 |
| 1971 | San Jose Island | 955 | Aransas NWR | 76 |
| 1979 | San Jose Island | 499 | Aransas NWR | 100 |
| 1985 | San Jose Island | 1,002 | Aransas NWR | 96 |
| 1990 | Matagorda Island | 486 | Aransas NWR | 24 |
| 1995 | San Jose Island | 1,191 | Aransas NWR | 39 |
| 2000 | San Jose Island | 717 | Aransas NWR | 28 |
| 2006 | San Jose Island | 853 | Aransas NWR | 38 |

2006, the largest territories were predominantly on San Jose Island, and the smallest average territory sizes occurred on Aransas NWR (109 ha) where the habitat was 90.3% occupied (Table 8).

The minimum average territory size appears to have changed little since 1990. Average minimum territory size is approaching 101 ha on Aransas NWR and West St. Charles Bay, 139 ha on Welder Flats, 204 ha on Matagorda Island, and 304 ha on San Jose Island. Average minimum territory size throughout the crane range was estimated to be 172 ha. Based on available contiguous habitat and minimum average

**Table 8. Occupied and adjacent unoccupied contiguous habitat (ha) during the 2006 winter in different areas at Aransas.**

| | Refuge | W. St. Charles | San Jose | Matagorda | Welder Flats | All areas | Carrying capacity (number of territories) |
|---|---|---|---|---|---|---|---|
| Occupied | 2,622 | 399 | 8,576 | 7,599 | 4,044 | 23,240 | 135 |
| Unoccupied | 281 | 1,493 | 780 | 2,843 | 102 | 5,499 | 32 |
| Total Habitat | 2,903 | 1,892 | 9,356 | 10,442 | 4,147 | 28,740 | 167 |
| % Occupied | 90.3 | 21.1 | 91.7 | 72.8 | 97.5 | 80.9 | 100 |

**Table 9. Carrying capacity of the habitat in different areas at Aransas for whooping cranes.**

| Area | Total habitat (ha) | Estimated minimum average territory size (ha) | Total no. of potential territories |
|---|---|---|---|
| Aransas NWR | 2,903 | 101 | 29 |
| W. St Charles | 1,892 | 101 | 19 |
| San Jose | 9,356 | 304 | 31 |
| Matagorda | 10,442 | 204 | 51 |
| Welder Flats | 4,147 | 139 | 30 |
| Totals | 28,740 | 180 | 160 |

territory sizes in each of the different crane areas, the carrying capacity at Aransas was calculated at 160 territories (Table 9).

## Number of Territories in Relation to Total Flock Size

For the 9 winters analyzed, the ratio of flock size divided by the number of observed territories averaged 3.6. In those years, with 2 adults in each territory, the flock consisted of between 45-71% adult cranes and averaged 56%. The remainder of the flock consisted of juveniles and subadults 1 to 3 or 4 years of age.

## Carrying Capacity

The estimated total number of territories ($n$ = 160) multiplied by 3.6 (to derive an average flock size) suggests there may be capacity for 576 whooping cranes in the main crane areas and adjacent habitat at Aransas. Additional salt marsh habitat was measured in a 111-km radius from Aransas NWR. If suitable, these non-contiguous areas (totaling 27,729 ha, Table 10) could support an additional 580 whooping cranes (on 161 territories), yielding a total flock size of 1,156 in the coastal region.

**Table 10. Expected future winter range expansion into non-contiguous areas for the Aransas-Wood Buffalo whooping crane population in Texas.**

| Area | ha |
|---|---|
| San Antonio-Nueces Coastal Basin | 14,368 |
| Lavaca-Guadalupe Coastal Basin | 1,224 |
| Colorado-Lavaca Coastal Basin | 8,266 |
| Brazos-Colorado Coastal Basin | 3,871 |
| Total | 27,729 |

# DISCUSSION

## Territory Establishment and Range Expansion

As the crane population increased from a low of 15 in 1941 to 266 in 2007, the size of the winter range slowly expanded. All pairs have established territories in proximity to the San Antonio-Guadalupe and northern portion of the Mission-Aransas River estuaries rather than moving long distances to other portions of the Texas coast.

Territories have spread outwards from core areas in an orderly fashion without large gaps of unoccupied marsh. There is a strong tendency of the species to establish territories next to other whooping cranes rather than to seek isolation. This must be part of the social nature of whooping cranes even though they carve out, defend, and maintain exclusive use of a territory in both summer and winter. Offspring (especially males) from resident pairs have a strong tendency to establish territories next to their parents (Stehn and Johnson 1987). This behavior explains most of the pattern of gradual

range expansion seen over the past 72 years. Since cranes in all of the major crane winter areas have supported numerous family groups, the number of territories has increased in all areas. Future range expansion will be influenced by which pairs successfully bring chicks to Aransas (Stehn and Johnson 1987), as well as by availability of unoccupied habitat.

New crane pairs looking to establish a winter territory fill in the unoccupied "empty" spaces between defended territories in the crane range if available. If no empty spaces exist between territories, whooping cranes may establish a territory in contiguous habitat at the ends of the crane range where no territories exist. When contiguous habitat becomes nearly fully occupied, cranes colonize into nearby non-contiguous areas. New adult pairs that colonize, rather than establishing territories in limited space next to other cranes, presumably benefit from the larger amount of unoccupied habitat available.

From the first territory on San Jose Island's northwest end, new territories have generally been established sequentially in adjacent unoccupied salt marsh to the southwest. At Welder Flats, new territories were generally established moving in a northeasterly direction from the initial territory. From the 3 territories present on Matagorda Island in 1979, the crane range expanded sequentially in northwesterly and/or southeasterly directions with multiple new territories. Stehn and Johnson (1987) predicted correctly that more territories would become established on Matagorda Island in the existing occupied range as well as expansion at both ends of the island's crane range.

The large expansion of the whooping crane winter range can be illustrated by changes in census flights with the primary author as observer over the past 26 years. Flights in the early 1980s were done in a Cessna 150, a small and slow aircraft that took approximately 3 hours to cover occupied crane range. Due to the limited distribution of the cranes at that time, flights on San Jose only covered the north end of the island, south to Long Reef. On Matagorda Island, flights did not cover the extreme south end of the island, nor did they cover the 33.8 km of salt marsh between Panther Point and the north end of the island since cranes rarely, if ever, used those areas. In 2006, using a faster Cessna 210, census flights required 7 hours to cover the occupied range. All of San Jose north of Allyn's Bight was flown. On Matagorda, the entire south end of the island was covered on every flight, along with an additional 26.7 km of habitat north of Panther Point. Only the extreme north end of Matagorda Island north of the abandoned military base was considered unoccupied range, although cranes have occasionally been sighted there, necessitating occasional survey flights of the area.

Since most of the coastal salt marshes along the edge of the mainland and barrier islands lie in relatively narrow strips, changes over time of the linear distance between ends of the occupied crane territories often provide a better picture of range expansion than total territory size. Most whooping crane territories front on a bay. Only in the widest portions of San Jose and Matagorda islands are territories permanently situated in the interior portions of the salt marsh without open bay habitat. At Aransas NWR newly established territories have occasionally not included bay frontage because the new pairs were presumably not as dominant as established pairs and were only able to establish smaller territories wherever marsh was available. Territories on Aransas NWR without frontage on the bay have not persisted over more than a few winters.

## Minimum Territory Size and Carrying Capacity

Territory size is limited by social interactions as neighboring cranes defend adjacent territories. Established territorial pairs do not allow other cranes to remain in their territory. Pairs normally respond quickly, flying towards the intruding cranes and driving them out with a show of aggression. Adjacent crane pairs are very aware of each others' presence (Stehn and Johnson 1987) and often unison call at dawn (B. Wessling, Ormecon International, personal communication). Establishment of a territory presumably provides the pair with food resources needed for survival. Upland areas next to territories that contain additional food resources and sources of fresh water to drink are typically not defended, although dominance behavior is frequently observed in those areas. A pair may use nearby portions of a neighboring pair's territory if their neighbors are located at the far end of their territory. At the beginning or end of migration periods when some territories are vacant, cranes at Aransas will frequently be located in an adjacent empty territory (Stehn and Johnson 1987). Adult cranes are often on a neighbor's territory about 50% of the time until the territorial pair arrives. Such wandering is rarely observed when all territorial cranes are present. When in a neighbor's territory, cranes are not depleting the food

resources in their own territory, but continue to monitor their own territory for intruding cranes.

There is evidence that winter territories reach a minimum size. Crane use has occurred along the refuge's east shore marshes at least since the late 1930s (Stehn and Johnson 1987). There have been pairs on the Blackjack Peninsula at Mustang Lake, Mustang Slough, Sundown Bay, and Dunham Bay for the length of this study and have been occupied for at least the past 72 years. Allen (1952) delineated 14 territories in 1950 that averaged 176 ha in size on Aransas NWR. However, these were not all permanently defended territories since the population only contained 7 breeding pairs. Allen had no way of identifying what were later described as subadult cranes. Blankinship (1976) mapped 10 territories in the same area that averaged 176 ha in size during the 1971 winter. In 1982, territories for that area were smaller, averaging 117 ha with the smallest only 55 ha in size (Stehn and Johnson 1987). Newly formed pairs, however, are sometimes not as dominant as long-established pairs and may initially have smaller territories (Stehn and Johnson 1987). In this study, the average size of territories in that area reached a low of 101 ha in 2000 and increased slightly to 109 ha in 2006.

We postulate that with little available habitat remaining on the refuge, territory size is approaching a minimum since the number of territories in that area has increased by only 2 between 1990 and 2007, and territory size has not changed much since 1982. That new pairs have expanded to other areas in the crane range, rather than continue to squeeze into smaller and smaller territories at Aransas NWR, indicates a minimum average territory size threshold is being reached. Thus, the almost fully utilized marshes on the Blackjack Peninsula and other portions of the wintering area provide insight into what may be the carrying capacity of coastal salt marsh for whooping cranes at Aransas.

The estimated minimum territory size at Aransas NWR of 101 ha averages approximately a third that of territories on San Jose and a half that on Matagorda. Differences in average territory size in different parts of the crane range may indicate differences in quality of whooping crane habitat. Larger territories might indicate that habitat in those areas is not as suitable for cranes. The largest territories for an area in this study occurred in 1990 on San Jose Island approaching 500 ha in size. San Jose Island consists of large tidal flats, more than half of which go dry during mid-winter periods of wind-blown tides, which presumably results in cranes needing larger territories in those areas. The diversity of habitats on the east shore of Aransas NWR with bay and upland habitats nearby provides what seems to be excellent habitat for cranes, presumably the best at Aransas. This is where the species wintered when the flock was reduced to only 15 birds in 1941, and where the territories are the smallest.

Territories must be of a sufficient size to support the occupants and at some point cannot continue to shrink as has been the long-term trend. The fact that the minimum average territory size for all parts of the winter range appears to have changed little since 1990 provides insight that a minimum average territory size is being approached. We acknowledge uncertainty as to what the exact future minimum average territory size will be. The 172-acre figure selected for this paper is close to the calculated figure of 180 ha and assumes territories may continue to shrink only a little from their current sizes.

Since the salt marsh habitat has to support subadult as well as adult whooping cranes, projecting carrying capacity based on the average minimum territory size of adult pairs may be an overestimate. Another way to estimate carrying capacity is to note that the occupied species range in 2007 of 23,240 ha supported a flock size of 266 cranes, or 87 ha per bird. Thus, the additional 5,499 ha of adjacent unoccupied habitat would support 63 more birds, for a total flock size of 329 cranes. This is a lower estimate derived than the 576 cranes (160 territories) based on average minimum territory sizes. Thus, the current range and contiguous unoccupied habitat at Aransas will reach carrying capacity at somewhere between 329 and 576 whooping cranes. However, any estimate of carrying capacity assumes that habitat quality will remain the same over time. This is unlikely given the threats on the Texas coast facing the species.

## Predicted Range Expansion

The amount of contiguous unoccupied habitat in the different parts of the crane range provides insight as to where the greatest number of future territories may be established. In 2006, contiguous unoccupied habitat on Matagorda Island (2,843 ha) and West St. Charles (1,492 ha) are where the most new territories are likely to be established. Stehn and Johnson (1987) noted that the cranes occupied 8,172 ha of salt marsh, or 26.8% of the available acreage. In 2006, the 23,240 ha of habitat used

took up 80.9% of the available contiguous habitat, an indication that carrying capacity is being approached in contiguous areas.

Another key to predicting the location of future range expansion is use of an area by subadults (Stehn and Johnson 1987) which is also indicative of habitat suitability. Whooping cranes ages 1 to 4 years frequently use areas next to defended territories. They spend a high percentage of their time in the vicinity of their first winter territory, although some wandering occurs between different parts of the winter range. Subadults may move several kilometers to where there is a gap between defended territories until they find an area where they are not chased by territorial pairs. When in larger groups, subadults can sometimes persevere and remain next to a pair's territory, or may use 1 end of a territory if the territorial pair is at the other end. Subadult cranes sometimes use areas generally apart from other cranes.

A current example for an area expected to support whooping crane territories is the extreme north end of Matagorda Island at the end of the current crane range where subadult use has been documented occasionally. Subadult crane use has also been documented on non-contiguous areas including the Tatton Unit, the mouth of Copano Creek, the northwest end of Hynes Bay, and by the town of Indianola.

No crane use has been documented on the south end of San Jose Island south of the Bass family ranch house, but the habitat appears suitable. At the end of the fall migration, cranes occasionally have been documented on Mudd Island and in Redfish Bay south of the current range, and across from the south end of San Jose. These areas may be colonized in the future. Black mangrove (*Avicennia germinans*), however, grows extensively in that area. In the past, the northernmost range of mangrove stopped just south of the whooping crane winter range, except for scattered colonies as far north as Galveston, Texas. Starting in the 1990s, with no prolonged hard winter freezes to limit the northward spread, mangrove is now found in portions of the current crane winter range on northern portions of Matagorda Island. This presumably makes the habitat less suitable for whooping cranes, and could increasingly become a major threat to whooping cranes if predicted climate change reduces winter freezes at Aransas.

Whooping cranes have never colonized the Guadalupe River Delta, a 1,815-hectare marsh located between Aransas NWR and Welder Flats 13.4 km north of the refuge crane range, where only a few documented sightings have occurred. The large number of wading birds and the presence of blue crab in the shallow marshes of the Guadalupe Delta make it appear to be potential whooping crane habitat. Stehn and Johnson (1987) speculated that future flock expansion would occur in that delta, but this has not yet happened. The area is less saline than the more brackish marsh at Aransas currently used by whooping cranes. It also has areas of taller vegetation consisting of common reed (*Phragmites australis*) that would limit visibility. One notable feature of the current range is the absence of any marsh vegetation that is taller than a whooping crane, a unique feature compared with most marshes in the eastern U.S. (F. Chavez, Platte River Whooping Crane Maintenance Trust, personal communication). Short vegetation provides excellent visibility for whooping cranes and protection from predators. Thus, the Guadalupe Delta may not be as suitable for whooping cranes as the current range.

Juvenile whooping cranes that have occasionally become separated from their parents in their first fall migration have wintered with sandhill cranes in inland areas in Texas and Oklahoma. In 1985, 1 subadult whooping crane that had never been to Aransas wintered partly in brackish marsh habitat 161 km up the coast from Aransas in Brazoria County, Texas (Lange 1992). This is the only example of a whooping crane separated from its parents utilizing brackish marsh habitat, but provides some evidence that habitat up the coast from Aransas could support whooping cranes in areas where whooping cranes occurred historically (Allen 1952). If flock growth continues, whooping cranes may expand north onto Matagorda Peninsula in Matagorda County and into marshes at the mouth of the Colorado River in Colorado County. The strong tendency for whooping cranes to establish territories next to other cranes, however, makes it unlikely that areas far up the coast will be used any time soon.

Once carrying capacity is reached in the current range including contiguous unoccupied habitat, additional dispersal to non-contiguous areas would be anticipated. Recovery would be aided if the location of these areas could be predicted. Using aerial infrared photography, apparently suitable salt marshes were identified beyond the current crane range. A 111-km search radius from the refuge's Mustang Lake was used to identify general areas of suitable habitat. This distance was selected based on observations made on commercial air flights along the

coast from Corpus Christi to Galveston. Few large blocks of suitable habitat occurred beyond a 111-km radius. Areas identified are not presented on a map since efforts to protect some of these areas might be hindered during possible future land negotiations.

From south to north, apparently suitable whooping crane habitat may be available in the Nueces River Delta just northwest of Corpus Christi, in Redfish Bay, and on the northwest portion of Padre Island. In the Lavaca-Guadalupe Coastal Basin, potential areas north of Aransas Pass include salt marshes on the edges of Port, Mission, Hynes, and Copano bays, and in the Guadalupe River Delta. In the Lavaca-Guadalupe Coastal Basin, potential habitat is present near Powderhorn Lake, Indianola, and Carancahua and Keller Bays. Areas of salt marsh in the Colorado-Lavaca Coastal Basin are located southwest of the mouth of the Colorado River and on the mainland west of Matagorda Peninsula, which includes the Mad Island Nature Preserve. The northernmost notable amount of suitable habitat is located northeast of the mouth of the Colorado River as far north as the Big Boggy NWR in the Brazos-Colorado Coastal Basin.

The Nueces River Delta is located approximately 84 km south of Aransas NWR, whereas the Colorado River Basin marshes are located 111 km to the north. Thus, the cranes would have to range along a 195-km stretch of the coast, compared to 69 km in 2007.

Expansion into non-contiguous areas to the south of Aransas is less likely than northern areas given the migration pattern of the species. Whooping cranes at the end of the migration are rarely found south of Aransas, and only a few documented sightings are reported as far south as Flour Bluff, Texas, located on the southern edge of Corpus Christi. The species thus would have less opportunity to encounter suitable habitats south of Aransas. No whooping crane use has ever been documented in the Nueces River Delta near Corpus Christi, although portions of that habitat appear suitable for cranes.

The size of additional non-contiguous areas of apparently suitable salt marsh habitat totaled 27,729 ha within the search area. Given enough time and with continued growth of the whooping crane population, it seems feasible that someday these areas would support whooping cranes. Assuming an average minimum territory size for these areas of 172 ha, these non-contiguous areas would provide room for an additional 161 territories, or 580 cranes. Thus, when added to the current habitat at Aransas plus contiguous unoccupied habitat that is estimated to support a maximum of 576 cranes, the entire area could in theory support a maximum of 1,156 cranes. This assumes development of these non-contiguous marshes and adjacent uplands does not occur, which is unlikely. Only 1,817 ha of the 27,729 ha (6.6%) where future winter range expansion into non-contiguous areas may occur are in public ownership and protected as wildlife areas from future development.

While habitat at Aransas is a major issue for recovery, habitat on the nesting grounds in Canada does not appear to be as limited. Wood Buffalo National Park and vicinity is estimated to be able to support between 185 and 426 new nesting territories in addition to the 72 territories already occupied. Thus, the carrying capacity of the nesting area may be somewhere between 257 and 498 territories (Olson and Olson Planning and Design Consultants Inc. 2003). Multiplying these numbers by 3.6 to derive flock size provides an estimate of carrying capacity in Wood Buffalo for a flock of between 925 and 1,793 birds before the cranes would disperse into habitat further removed from the current nesting area.

## Human Development

Rapid human population growth is expected on the Texas coast. Development pressure next to crane areas intensified starting in about 2005. Crane salt marshes on the Lamar Peninsula and Welder Flats are in areas where development is now occurring. Four canal lot subdivisions are either currently under construction or in the permitting phase and will place over 1,500 homes in or adjacent to areas used by whooping cranes. The presence of cars, houses, people, and boats next to occupied crane marshes will remove portions of habitat from use by the species due to increased human disturbance. An immediate need is to protect salt marshes by purchasing lands or conservation easements where cranes occur or are expected to occur. Upland buffers are needed next to salt marshes to provide areas for cranes for foraging and drinking water, and to limit human disturbance by keeping new houses away from the edges of the salt marsh. Such buffers would also allow new marsh to be created as sea level rises. Upland buffers need to be a minimum of 100 m wide, but ideally would be up to 1,000 m wide, the distance that human disturbance of whooping cranes has been documented (T. Lewis, U.S. Fish and Wildlife Service, unpublished data).

In 2007, of 23,240 ha of occupied whooping crane range, 12,811 ha (55.1%) were on private land. Public land on Aransas NWR, the refuge's Lamar Unit, and Matagorda Island totaled 10,429 ha (44.9%). These lands in State or Federal ownership are designated wildlife areas and are protected from development. Private lands occurred on San Jose Island, Welder Flats, and portions of West St. Charles. All of San Jose Island is owned by the Bass family which has provided an excellent place for whooping cranes and hopefully will remain so for many years to come. San Jose is managed as a working cattle ranch with grazing, mowing, and prescribed burning. The only developments on the island are the Bass family ranch house complex, airplane runway, a single road through the uplands the length of the island, and various fences, pens, and dugouts for management of cattle. The ranch house currently marks the southernmost extent of occupied range on San Jose.

As more people live in south Texas, more hunting, fishing, bird-watching, and nature photography will occur in crane marshes, increasing levels of human disturbance. Airboats and kayaks have allowed people to traverse shallow water areas. Maintaining water quality and productivity of the bays in the crane area will be extremely difficult as the coast becomes intensely developed and salt marshes are impacted.

The presence of more people on the Texas coast will also increase the pressure to divert more water for human consumption from the San Antonio, Guadalupe, and other rivers. Decreased river inflows will reduce the suitability of the bays and salt marshes at Aransas for blue crabs, the primary food of the whooping cranes during winter. It is essential for the survival of the species that adequate inflows be maintained to enable the estuary to remain productive.

## CONCLUSIONS

Habitat at Aransas appears to be a key limiting factor for long-term growth of the whooping crane population. There is sufficient habitat at Aransas to support a minimum of 40 mated pairs, a prime objective in the 2007 International Whooping Crane Recovery Plan (CWS and USFWS 2007). However, there is only enough available habitat within a 111-km radius of Aransas NWR to support slightly more than 1,000 whooping cranes, the threshold number needed to be reached for consideration of downlisting the species to "threatened" if additional separate flocks of whooping cranes cannot be established elsewhere. With suitable habitat at Aransas expected to limit recovery, it is essential that as many of the existing marshes as possible receive protection so that the carrying capacity of these marshes is not reduced by development. With a target level of 1,000 whooping cranes expected to take more than 25 more years to achieve, recovery remains a distant goal. With no de-listing target set by the International Whooping Crane Recovery Team, a total population of between 5,000 and 7,000 whooping cranes might be a reasonable estimate for numbers needed to remove the species from the Endangered Species list. The winter area needed to support such population numbers is beyond the scope of this study, but it is not available within a 111-km radius of Aransas.

At Aransas, in addition to having sufficient habitat acreage available, it is imperative that management efforts maintain the environmental quality of the habitat (Stehn and Johnson 1987). All marsh areas along the Texas coast are threatened with sea level rise and land subsidence, which are ongoing and forecasted to continue. Marshes on undeveloped areas such as Aransas NWR and Matagorda and San Jose islands currently have room to move inland so that total marsh acreage on those areas may remain relatively constant in this century. Marshes next to developed areas probably will not be able to move inland due to bulkheads likely to be built to protect housing developments. The Texas Nature Conservancy, in close partnership with other agencies, has begun trying to purchase upland buffers next to whooping crane areas to provide room for marshes to move inland and to limit human disturbance. This effort needs to be funded, expanded upon, and accelerated before more of the anticipated development occurs.

Whooping crane habitat at Aransas is threatened by multiple factors including human development, increased human disturbance, sea level rise, potential changes in rainfall patterns, reduction of river inflows at Aransas, and chemical spills along the Gulf Intracoastal Waterway. Threats to loss of migration habitat in the migration corridor are unquantified, but real. These threats include construction of power lines, loss of migration habitat from wetland drainage and reduction in river flows, tar sands development, and introduction of exotic diseases. Changes in farm programs and new developments including wind energy may reduce migration habitat available for whooping cranes. It is imperative that a

watchful eye be kept on the whooping crane population for many years to come to continue to allow this species to progress towards recovery.

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